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Ant Presence in Acacias: An Association That Maximizes Nesting Success in Birds?

Adán Oliveras de Ita^{1,3} and Octavio R. Rojas-Soto²

ABSTRACT.—Nest predation is the main cause of reproductive failure in birds, yet the factors that drive predation pressure, as well as the avian strategies to minimize it, are poorly understood. There is a wellknown commensal relationship between ants and birds nesting in acacia trees, but the direct benefit in terms of avian reproductive success has not been tested properly. We used artificial nests to compare success and survival probability of nests placed in Hinds' acacia trees (Acacia hindsii) associated with ants (Pseudomyrmex spp.) with those of nests placed in trees without ants. Nesting success and the probability of daily survival were greater in acacias than in antless trees. All cases of nest failure were due to egg predation, but none resulted from wren activities, as has been reported in previous studies. The results of this experimental study indicate that the presence of ants in acacias may enhance avian reproductive success by reducing the probability of nest predation. Received 30 June 2005, accepted 28 June 2006,

Several bird species of the families Formicariidae, Tyrannidae, Troglodytidae, and Emberizidae prefer to establish their nests in acacias with which *Pseudomyrmex* spp. ants associate (Janzen 1969, Young et al. 1990, Flaspohler and Laska 1994). The relationship between birds nesting in acacias inhabited by ants seems to be commensal, because ants that protect acacias against herbivores also offer protection against avian nest predators (Skutch 1945, Janzen 1983, Flaspohler and Laska 1994). On the other hand, birds do not seem to provide any benefit to acacias or ants (Gilardi and Von Kugelgen 1991).

It has not been proven, however, that a myrmecophytic association confers greater breeding success to birds. A study conducted in Costa Rica (Young et al. 1990) revealed a 36% failure rate of artificial nests (n = 50) placed in myrmecophyte acacias, but, in antless tress, only 18% (n = 49) of the nests failed (Young et al. 1990). Of the failed nests, 72% of those located in acacias and 44% of those located in antless trees failed due to egg destruction by Rufous-naped Wrens (*Campylorhynchus rufinucha*).

We conducted an experiment on the Pacific coast of Mexico using artificial nests to determine whether the myrmecophytic association confers a benefit to birds in terms of greater nesting success. We also examined whether nesting failure at our study site was related to egg destruction by species ecologically equivalent to the Rufous-naped Wren (Ehrlich et al. 1988, Dion et al. 2000)—Sinaloa Wren (*Thryothorus sinaloa*), Happy Wren (*T. felix*), and White-bellied Wren (*Uropsila leucogastra*).

METHODS

We conducted our study during September 2004 in the Chamela-Cuixmala Biosphere Reserve on the Pacific coast of Mexico (19° 30′ N, 105° 0.3′ W). Tropical dry deciduous forest is the dominant vegetation, and acacias generally occur as secondary growth in locally distributed sites near the coast. We collected data at two sites characterized by similar vegetation: Careyes and Negritos, situated southeast and northeast, respectively, of the Biological Station. We randomly selected a 1-km transect at each site and placed 28 artificial nests along each transect: 14 in Hinds' acacia trees (Acacia hindsii) and 14 in antless trees. The cup-shaped nests were placed 1.7-2.2 m above ground and wired to the tree trunks. In each nest, we placed three hand-made eggs (20-mm length)—made of white plasticine and sprayed with varnish—to resemble eggs

¹ Centro de Investigaciones en Ecosistemas (CIE-CO), Univ. Nacional Autónoma de México, Antigua Carretera a Pátzcuaro No. 8701, C.P. 58190, Morelia, Michoacán, México.

² Instituto de Ecología, A.C., Depto. de Biología Evolutiva, km 2.5 Carretera Antigua a Coatepec No. 351, Congregación el Haya, C.P. 91070, Xalapa, Veracruz, México.

³ Corresponding author; e-mail: oliveras@laneta.apc.org

of the Social Flycatcher (*Myiozetetes similis*). Social Flycatchers are common breeders in the area and reportedly nest in acacias (Pettingill 1942). Predators readily left marks in the plasticine, thus allowing us to identify predator species and the impact of wrens on nesting success, if any (Major 1991, Major and Kendal 1996, Dion et al. 2000, Zanette and Jenkins 2000).

Nests were exposed to predators for 6 days. We recorded egg condition every 2 days and removed those nests in which eggs showed evidence of predation. Based on previous reports (Kennedy and White 1996, Hannon and Cotterill 1998), wren species usually peck small holes in the eggs of other species. To determine whether wrens were responsible for nest "failure," we compared marks on the plasticine eggs recovered from depredated nests with those we made using the bills of museum specimens representing the three wren species that occurred in our study area: Sinaloa Wren, Happy Wren, and White-bellied Wren.

The percentage of nests in which no eggs showed damage by the end of our experiment was our measure of nesting success. To determine differences in failure probabilities between sites and tree type in which nests were located, we analyzed the data with a linear generalized model (GENMOD), assuming a binominal distribution and a logit function (SAS Institute, Inc. 2000). The independent categorical variables were our two sites (Careyes and Negritos) and the two tree types (myrmecophyte acacia or antless tree); in both cases the dependent variable was the probability of nest failure.

We calculated daily survival rate (DSR), by tree type, using the daily probability of nest survival. Survival rate—the most reliable measure of nesting success (Ralph et al. 1996)—was calculated with the MAYFIELD program (Hines 1996) based on the method proposed by Mayfield (1961, 1975) and revised by Bart and Robson (1982). Differences in DSR means were assessed with a Z-test using variances obtained from the MAYFIELD program. Means are reported ± SE.

RESULTS

Nest success was similar at both sites (39% at Careyes and 43% at Negritos; $\chi^2 = 0.15$, P

= 0.70, df = 1). However, nest success was greater for nests placed in acacias (64.3%) than those placed in antless trees (17.8%; χ^2 = 13.06, P < 0.001, df = 1). Because there was no site effect, we pooled our data for calculating DSR estimates. DSR was greater for nests located in acacias (0.944 ± 0.017, n = 28) than it was for those located in antless trees (0.808 ± 0.036, n = 28; Z = 10.73, P = 0.010). Overall nest survival (6 days of exposure) was 70.5% (n = 28) in acacias, and 28% (n = 28) in antless trees. All nest failures were due to predation; however, based on our observations of marks left on the plasticine eggs, no eggs were destroyed by wrens.

DISCUSSION

Our results indicate that the type of tree where nests were placed (acacias versus antless) affected the probability of nest success. Probability of survival was greater for nests placed in acacias, which may be related to the presence of ants. This supports Skutch's (1945) hypothesis, which suggests that nests in acacias have a higher probability of survival due to the ants that associate with them, despite the minimal cover that acacias provide for nest concealment (Young et al. 1990). The results of previous studies with artificial nests of other species indicate that egg predation may be greater where canopy cover is minimal (Crabtree et al. 1989, Sullivan and Dinsmore 1990, Mankin and Warnen 1992, Martin 1992; but see Gottfried and Thompson 1978). Although we did not measure canopy cover around the nests, egg predation was not greater under the poor canopy cover that characterizes Acacia spp. Indeed, low rates of egg predation in acacias—despite their minimal foliage cover—underscores the potential role of ants in providing protection against nest predators.

In Costa Rica, the success rate of artificial nests placed in acacias (64%; Young et al. 1990) was similar to the rate we detected at Chamela (64.3%), but the percentage of successful nests in antless trees was much greater (81.6%) than it was at Chamela (17.8%). In addition, we found no evidence of wren predation on eggs, though longer observation periods may be necessary to confirm this pattern. The low rates of success that we observed for nests placed in antless trees (en-

tirely due to predation) suggest that, in the absence of Rufous-naped Wrens, acacias with which ants associate increases the probability of avian nest survival, despite of the presence of other wren species.

Previous researchers have proposed that birds reduce the probability of nesting failure by minimizing parental activity around the nest (Martin et al. 2000); producing smaller clutches to minimize parental activity (Skutch 1949, 1976) or to save energy for a second brood (Slagsvold 1982); evolving shorter incubation periods (Ricklefs 1969; but see Martin 2002); and/or nesting at the end of the dry season (Morton 1971, Poulin et al. 1992). Janzen (1969) and Young et al. (1990) found that several species were more likely to nest in acacias than in antless trees. Consistent with these observations, our results indicate that artificial nests located in acacias with ants have greater probabilities of nest survival. Thus, we propose that this may be yet another strategy for maximizing nest success.

Unfortunately, no antless acacias were available at our study sites; evaluations of nest success in antless acacias will be necessary to confirm the role of ants in discouraging predation. In addition, evaluating the effects of different acacia species, canopy cover, and the possible influence of different ant species on nest success will provide better insights into the mechanisms behind enhanced nesting success in acacias with which ants associate.

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Pair Roosting of Nesting Carolina Wrens (Thryothorus ludovicianus)

Ronald F. Labisky^{1,2} and John E. Arnett, Jr.¹

ABSTRACT.—Carolina Wrens (Thryothorus ludovicianus), which maintain lifetime pair bonds and yearround territories, huddle in pair or communal roosts during the non-breeding season, particularly during cold winter nights. Pair roosting during the nesting season, however, is not known to occur. Here, we report huddled pair roosting by Carolina Wrens in Florida. The dates of pair roosting took place during nest construction through laying of the first egg (9-20 March 2004), and also on the date the fourth egg was laid in a clutch of five (24 March). The wrens roosted in a hanging flower basket located 2.4 m from their nest site. Although huddled pair roosting by wrens during periods of low ambient temperatures in the nonbreeding season likely achieves thermal conservation, the benefits derived during the breeding season remain unclear. We discuss the possible thermoregulatory and pair-bond maintenance functions of pair roosting. Received 6 September 2005, accepted 5 July 2006.

Roosting by two or more birds has been hypothesized to ameliorate the energetic cost of thermoregulation during cold temperatures, lower the risk of predation, and improve foraging efficiency (Beauchamp 1999). Numerous researchers have examined pair, communal, or huddled roosting during the non-breeding season (in cavities: du Plessis and Williams 1994; in dormitory nests: Sharrock 1980, Gill and Stutchbury 2005; in foliage: Balda et al. 1977). Yet, the occurrence and function of these types of roosts during the breeding season remains a poorly understood aspect of avian behavior.

The Carolina Wren (Thryothorus ludovicianus) is the only Thryothorus wren whose range extends beyond tropical latitudes (Morton 1982). In contrast to wren species with which it is sympatric in North America, Carolina Wrens form lifetime pair bonds and defend a territory throughout the year (Morton and Shalter 1977). They also roost in a variety of natural and anthropogenic structures (Haggerty and Morton 1995) and are known to roost in pairs during the non-breeding season (Brooks 1932, Tamar 1980). Whereas some tropical wrens form communal or pair roosts throughout the year (Skutch 1940, Robinson et al. 2000, Gill and Stutchbury 2005), to our knowledge there are no reports of pair roosting during the breeding season for tropical or temperate populations of Carolina Wrens. Laskey (1948) assumed that both members of a

¹ Dept. of Wildlife Ecology and Conservation, Univ. of Florida, P.O. Box 110430, Gainesville, FL 32611, USA.

² Corresponding author; e-mail: labiskyr@ufl.edu